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Progress Report

VARIABLES AFFECTING THE CAPACITY OF BARK BEETLES TO DAMAGE TREES

1962 Studies

By

William D. Bedard

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U. S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE
PACIFIC SOUTHWEST FOREST AND RANGE EXPERIMENT STATION

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SUMMARY

Preliminary studies on variations in the host-finding capacity of the western pine beetle, Dendroctonus brevicomis LeConte, were conducted at the Stanislaus Branch Station in the central Sierra Nevada Mountains.

Beetles from different sources were marked and released out-of-doors near attractive traps. The recovery of beetles in these traps was taken as an indicator of their host-finding capacity. Too few cage-emerged beetles were recovered to allow this measurement to be an acceptable performance test of host-finding capacity.

The reasons for this failure were sought in both laboratory and field experiments and observations. Obvious errors in the technique were investigated. The possible effect of marking, attractant saturation, and release point were investigated. None was found to be an obvious impediment to guided flight. The technique was found successful with wild, trapped beetles.

Therefore, the difference between wild, trapped beetles and cage-emerged beetles was sought. Walking phototaxis, walking chemotaxis, and degree of distention of the proventriculus were used as a basis for comparison. The only difference found which is not attributable to differences in post-emergence age (the wild, trapped beetles being the older) was walking chemotaxis. But, this difference was small compared to the difference in field tests. An attempt was made to increase the field host-finding response of caged-emerged beetles through tethered flight exercise. It was unsuccessful.

Many insect associates of the western pine beetle were trapped in the attractive traps.

The recovery of cage-emerged beetles was increased by changing the locations of the traps, increasing their attractive charge, and allowing the beetles to age in cold storage instead of under laboratory conditions.

The toss test and the tether test were tried as alternative methods of comparing the host-finding capacity of beetles.

The configuration of the frons was found to be a useful way to sex living western pine beetles.

INTRODUCTION

Each year bark beetles kill and injure many trees in California. The loss in timber volume and grade plus control costs were estimated at $33,980,000 for 1960. In addition to monetary loss bark beetle-killed trees decrease the recreational value of stands and increase their fire hazard.

Past research aimed at minimizing bark beetle loss has been concentrated on variables associated with host trees or with climate and weather. Silvicultural and forest managerial practices based on this past research have failed to lower bark beetle damage to an acceptable level. Our goal is to investigate a third area of variables, those associated with the bark beetles themselves, in order to make our action programs more effective and efficient.

The first group of variables associated with bark beetles to be investigated are those affecting the capacity of different populations to reach their prospective host trees. Our initial goal is to find and isolate differences in the flight and host-finding capacity of different populations by comparing their host-finding flight success under natural conditions.

Inasmuch as this is the first adventure into this problem area, the results should be interpreted with this in mind. They should be considered exploratory, not definitive. The value of these findings is best measured in terms of their utility to further research in the problem area rather than their potential application to other research or field practice.

MATERIALS AND METHODS

Study area.--These studies were conducted at the Stanislaus Branch Station of the Pacific Southwest Forest and Range Experiment Station. The Branch Station is located near Strawberry, California, which is on State Highway 108, 32 miles northeast of Sonora. The elevation at the Station is 5,200 feet. Mature, westside mixed conifer forest with openings and new growth is the predominant vegetation. The Station lies in the bottom of a valley with slopes rising 1,000 feet above on both sides.

Test animal.--The western pine beetle, Dendroctonus brevicomis LeConte, was used exclusively in this work. Ten different broods were collected from different localities representing variation in both trees and tree environments. Infested bark was taken from the lower bole of trees when the insects were in the early brood emergence stage. Collection data were taken in case they might be correlated with differences in beetle performances. These data included physical form of the tree and its site plus a rough history of recent western pine beetle activity in the immediate area.

Broods were reared from the infested bark in two ways: (1) in cardboard boxes (Lyon 1963),[1] and (2) in screen cages (fig. 1, C and D, respectively). Both types of containers were outside in full sunlight. They were elevated to provide protection from ants and high temperatures near the ground. The cardboard boxes were partially shaded by a snowfence roof. Small western pine beetles escaped from the screen cages through the normal gaps between strands of the screen (16 mesh per inch). Diurnal-ambient air temperatures near the cages generally ranged from a high of 80° F. to a low of 40° F. The boxes were usually 8° F. higher during the day but returned to the same lows as ambient air at night.

Beetles were collected daily starting at 4:30 p.m. They were captured and held individually in gelatin capsules. Capsules containing beetles were held under laboratory conditions of fluctuating daily temperatures (maximum 70° F., minimum 50° F.) and light.

COMPARISON OF HOST-FINDING SUCCESS UNDER FIELD CONDITIONS

PROCEDURE

The success of host-finding flights was measured by recovery of marked, liberated beetles in attractive traps. Beetles were marked on the pronotum with a small spot of fluorescent lacquer. The lacquer was applied with a fine, blunt pin under ambient temperatures around 60° F. and placed in an uncovered releasing tray. Up to 300 beetles were released simultaneously from a single tray 20 yards downwind from the attractive traps. This was accomplished by a sudden sharp flipping movement of the tray 10 feet above the ground. The action of the flipping movement tossed the beetles up into the air. Beetles which did not fly were caught on white, cotton sheets placed on the ground under the release point. Beetles were given two such chances to fly. Halves of gelatin capsules with their opening up were glued to a board to serve as a releasing tray.

The attractive traps were facsimiles of the field olfactometers used by Vité and Gara (1962[2] (fig. 1, E and F). Our machines differed from those of Vité and Gara in the amount of air displaced per unit of time. Ours had less displacement and, therefore, possibly had reduced efficiency. The attractive quality emanated from successful attacks of female western pine beetles on small ponderosa pine, *Pinus ponderosa* Lawson, bolts (Vité and Gara 1962). Each bolt had at least 25 successful attacks. Up to four such bolts were used to stock each of our three olfactometers.

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[1] Lyon, Robert L. Progress Report, Chemical control of bark beetles, 1961 studies. U. S. Forest Serv., Pac. Southwest Forest and Range Expt. Sta., 65 pp., illus., 1963 (processed).

[2] Vité, J. P. and Gara, R. I. Volatile attractants from ponderosa pine attacked by bark beetles (Coleoptera: Scolytidae). Contrib. Boyce Thompson Inst. 21: 251-273, illus., 1962.

Data taken on these field flight tests included temperature, time of release, approximate range of wind speed and direction 6 feet above the ground, history of test beetles, and color of their markings.

RESULTS AND DISCUSSION

In the first five tests of host-finding flight success, only 0.8 percent of 380 beetles released was recovered in the attractive traps. With such low returns the technique was considered inappropriate for our purpose. Possible errors in the method were sought to explain these poor returns.

CHECKS ON TECHNIQUE

A cursory search was started to locate obvious errors in technique. Experiments were run to check the effect of paint on beetle mortality, attractant saturation on beetle chemotaxis, and release position in relation to attractive traps on recovery.

EFFECT OF PAINT ON BEETLE MORTALITY

Eighty beetles, all from one day's emergence of one population, were used to measure the possible toxicity of the fluorescent lacquer to beetles. Four replicates of 10 beetles each were painted in the usual manner (see above), and four replicates of 10 beetles each were used as controls. Beetles were stored individually in capsules pierced for ventilation. Mortality was recorded each day for 15 days following treatment. At no time was there a significant difference in mortality between painted and unpainted beetles.

Mortality is not a sensitive indicator of the possible role painting can play in interfering with normal flying chemotaxis. But it is reassuring to know that it is not deleterious to the point of mortality.

EFFECT OF ATTRACTANT SATURATION ON BEETLE CHEMORECEPTION

Test beetles were normally held in an atmosphere containing some attractant. Under such conditions the chemoreceptors of these beetles could become saturated or fatigued. Two experiments were designed and executed to test this possibility.

In the first experiment 107 beetles were divided into two groups. Fifty-four were held in a closed container with 20 successful attacks, and 53 were kept in an open container as a control. Both groups of beetles were held for 6 hours in a weather shelter $\frac{1}{4}$ mile upwind from the attractive traps. All beetles were released simultaneously near the attractive traps. The range in time from the "saturated" atmosphere to release was 2 to 7 minutes. The results were inconclusive because only one beetle was recovered.

A second method designed to show the possible effect of fatigued chemoreceptors on chemotaxis was tried. Observations were made on walking chemotaxes instead of flying chemotaxes. A simple laboratory olfactometer was built to test the response of both attractant "saturated" and attractant-"unsaturated" beetles. Two small, converging streams of air were passed across a plain surface. A chamber containing 25 attractive attacks was in the air supply to one stream; the other stream, without such a chamber, was the control. Orifice size and nozzle shape were the same in both lines, and pinch clamps were used to equalize air flow. An air compressor from a spray painter served as the air supply. Air from the compressor was sent through a simple heat exchanger to minimize the change in test air temperature as the compressor warmed up. Beetles were placed in the overlapping area of the stream facing downstream. In order to be classed as a positive responder a beetle would have to turn around and walk up the treatment stream. Beetles which were not classed as positive on their first trial were tested a second time.

Forty test beetles which had emerged the previous day from the same population were divided into two 20-beetle samples. One sample, the treatment sample, was placed in the chamber of the olfactometer containing the attractive attacks. The second sample, the control sample, was kept open in the laboratory. After $4\frac{1}{2}$ hours of this preconditioning the walking chemotaxis of each beetle was tested. Of the 20 attractant-"saturated" beetles, 14 were positive and 6 were indifferent. Of the 20 control beetles 15 were positive and 5 were indifferent. There does not appear to be any interference of chemotaxis by "saturation" effects when measured under the high concentrations used.

EFFECT OF RELEASE POINT ON RECOVERY

The location of the release point in relation to the attractive traps could have an effect on the chance of beetles finding the attractive trap. Beetles released upwind from the traps might fly against the wind and never contact any attractant. Beetles released too close to the traps might have too strong a tendency to disperse to respond readily to the attractant. Therefore, 120 beetles which had emerged the previous day from the same population were divided in 3 samples of 40 beetles each. One aliquot was released 300 yards downwind from the traps. The second was released 300 yards upwind from the traps. And the third was released at the attractive traps. Again, the poor return of released beetles precluded any conclusions. Only one beetle was recovered.

PERFORMANCE OF TRAPPED, WILD BEETLES

Wild western pine beetles, apparently from natural infestations in the study area, were caught in the attractive traps. This helped to verify the efficacy of the traps and also provided a further check on technique. The wild, trapped beetles were handled, marked, and released as in the standard technique to see if they could be recovered. Wild beetles were taken from the traps every hour, marked, and released. The time between finding the beetles in the traps and release was 10 minutes. Of the 19 wild beetles tested, 11 were recovered. The technique must be considered successful with wild, trapped beetles but not with cage-emerged beetles.

POSSIBLE INDICATORS OF HOST-FINDING FLIGHT PREDISPOSITION

One interpretation that can be made of this difference in beetles is suggested by the findings of Graham (1959 and 1961).3/ Graham reports that adults of *Trypodendron lineatum* (Oliv.) require flight exercise to release their host-finding responses from photic dominance. This release has a mechanical basis in the distention of the proventriculus. As the beetles fly they swallow air, and as this air distends the proventriculus the beetles become less apt to respond to light and more apt to respond to an attractive host. This mechanism provides morphological and behavioral indicators of a particular behavior pattern.

Three such indicators were explored with the western pine beetle in the hope that one might show when cage-emerged beetles were ready to make host-finding flights. The phototaxis, chemotaxis, and degree of distention of the proventriculus of trapped, wild and caged-emerged beetles were compared.

PHOTOTAXIS

Before flight exercise, *Trypodendron* exhibits a positive phototaxis. Flight exercise changes this response to photoindifference. The photic response of trapped and cage-emerged western pine beetles were compared to see if Graham's findings were applicable.

3/ Graham, Kenneth. Release by flight exercise of a chemotropic response from photopositive domination in a scolytid beetle. Nature 184: 283-284. 1959.

Graham, Kenneth. Air-swallowing: a mechanism in photic reversal of the beetle *Trypodendron*. Nature 191:519-520. 1961.

The method used to test the photic responses of beetles was as follows. Individual beetles were placed in the center of a 18 x 24-inch plain surface. The only illumination in the test room was a single incandescent bulb. Light from the bulb was directed to shine obliquely down on one end of the plain surface. This provided illumination predominately of one direction with a gradient of intensity. Each beetle was tested three times with a rest of 5 to 10 minutes between tests. A beetle was classed as photopositive if it walked toward the light in all three trials.

The photic response of recently trapped beetles is indifferent as measured by this technique. Most cage-emerged beetles are also indifferent. This measure of behavior is, therefore, not specific enough to separate beetles which are not prepared to make a host-finding flight (cage-emerged beetles) from those which are prepared (recently trapped beetles).

CHEMOTAXIS

The possibility that walking chemotaxis would reflect flying chemotaxis was examined. The walking chemotaxes of trapped and recently cage-emerged beetles was compared by the same method used to measure the effect of attractant "saturation" described above. Records of the daily performances in the laboratory for individual, cage-emerged beetles were kept. Such records could show when a beetle's response to the attractant was ready for field flight testing.

Twenty-six trapped beetles were tested and all but two were positive (92 percent positive). Twenty of the 34 newly, cage-emerged beetles tested were positive (59 percent positive).

The change in response with time in cage-emerged beetles (table 1) shows a trend; as the sample ages the percent of positive responses rises. (An exception to this is the effect of morbidity at extreme age reflected in the data for days 8 and 9 of population 2.) When the responses of individual beetles are followed through time, the picture is not as clearcut. There does not seem to be a discrete change in response from indifferent to positive. Many beetles positive one day would test indifferent the following day. However, as the massed data show the reverse change was more common.

Table 1.--Percent of positive walking chemotaxes in laboratory olfactometer

	Number of	Day(s) after emergence									
	beetles at start	0	1	2	3	4	5	6	7	8	9
Population 1	34	59	68	67	82	84	73	96	87	93	--
Population 2	40	53	47	70	69	67	77	78	83	73	72

Three types of data discredit the laboratory, walking chemotaxis as an indicator of field, flying chemotaxis: (a) a far greater percentage of beetles (one day after emergence) are classed as positive in the laboratory (ca. 60 percent) than were recovered in field tests (less than 1 percent) of comparable beetles; (b) by the time the beetles have aged to the point where the greatest proportion of them respond positively (one week) only half are capable of flight(see effect of aging below); and (c) the proportion of positive responders becomes very similar in cage-emerged beetles and trapped beetles. This is not in agreement with field flight tests.

A possible cause underlying the inadequacy of this laboratory measurement is the difference in attractant concentration between laboratory and field tests. If predisposition for host selection is understood in terms of thresholds and competing response systems, beetles could be forced to make a host selection by increasing the concentration of the attractant. This can be done in the laboratory olfactometer. "Indifferent" beetles placed closer to the source of attractant change to positive under the influence of the increased concentration. The high concentration of attractant in the laboratory olfactometer compared to the field olfactometer could account in part for the 60-fold difference in their respective measurements of beetle responses.

MORPHOLOGY

An initial comparison between degree of proventriculus distention in trapped and cage-emerged beetles was made. Degree of distention was established by vivisecting specimens held in wax under Yeager's cockroach saline. Proventriculi were classed as positive, negative, or intermediate according to the intersection of imaginary lines extended from the ridges of the anterior part of the proventriculus. If the lines intersected antrad, the proventriculus was classed negative (figure I, A). If they intersected caudad, the proventriculus was classed positive (figure I, B). And if the lines were parallel, the proventriculus was classed as intermediate. Records were also taken on the contents of the gut lumen of dissected beetles.

Seven different samples of beetles were dissected. Three samples were composed of beetles taken from infested bark. These beetles ranged in development from newly formed, callows to adults in the act of boring out to emerge. The first sample was dissected the day the beetles were taken from the bark. The second was dissected 3 days later. And the third was dissected 6 days after they had been taken from the bark. Two samples were of cage-emerged beetles. The first was dissected the day after emergence; the second was dissected 7 days after emergence. Two samples were of trapped beetles. In one the beetles were allowed to age before dissection, in another they were dissected within $\frac{1}{2}$ day of trapping.

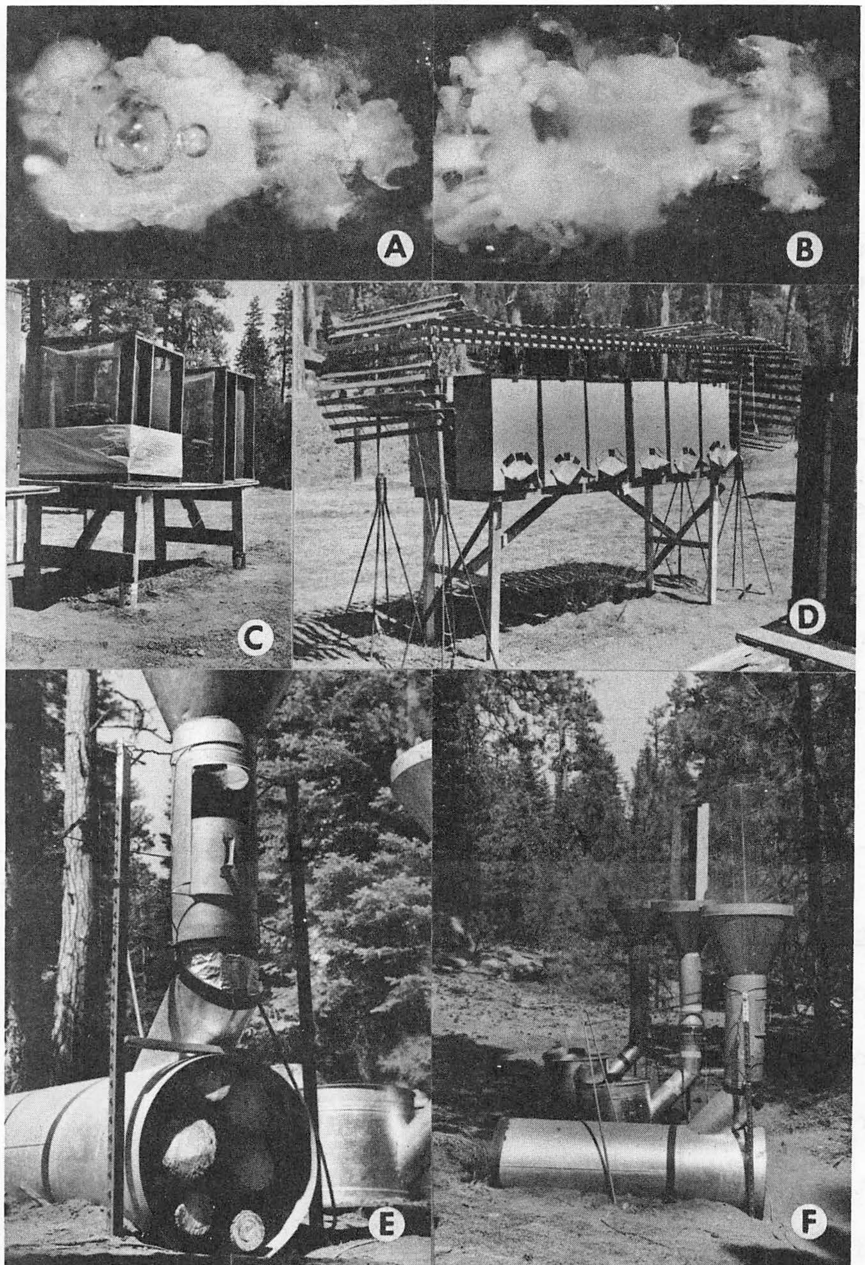

Figure 1.--A and B, Dorsal dissection of *Dendroctonus brevicomis* LeConte, head at extreme right, rectum at extreme left. A, Proventriculus undistended (called negative in text), midgut distended with two large gas bubbles. B, Proventriculus distended with one gas bubble (called positive in test), midgut void of gas. C and D, Cages used to rear test insects. C, Screen cages. D, Cardboard box cages. E and F, Attractive traps used to catch released beetles. E, Trap open to show charge of logs (containing attractive attacks) (lower opening) and collection jar (upper opening). F, Battery of three attractive traps in "new" location (see test).

The results (table 2) suggest two generalizations. One, proventriculus distention is not an indicator of host-finding predisposition in the western pine beetle as it is reported to be in Trypodendron. Two, there seems to be a pattern of proventriculus distention in adult ontogeny. This pattern and associated changes in the adult alimentary canal can be described as follows. Callow adults feed before emerging. At this stage the proventriculus and other parts of the foregut, along with the mid- and hindgut, are all filled with red-brown bark tissue. When feeding stops the reddish residue is progressively cleared from the alimentary canal until only the rectum contains the residue. Within a few days the red residue in the rectum turns yellow. As the solid material leaves the gut only fluid remains. At this stage gas begins to appear in the fore- and midgut of many beetles. The amount of gas increases in the midgut of some until up to one-half of the volume of the abdomen is gas (figure I, A). This is the internal condition of many emerging beetles. The presence of this gas phase in the ontogeny of adults was common in the beetles studied but apparently is not obligatory. Some trapped beetles (ready to attack) were found completely void of intestinal gas.

Table 2.--Degree of distention of the proventriculi of beetles from different sources

Origin of sample	Number observed	Number of proventriculi classed-- Positive	Negative	Intermediate
Taken from bark; aged 0 days	15	[1]/8	7	--
Taken from bark; aged 3 days	13	7	6	--
Taken from bark; aged 6 days	15	5	9	1
1 day after emergence	15	5	10	--
7 days after emergence	15	11	2	2
Wild, trapped; aged $<\frac{1}{2}$ day	23	6	14	3
Wild, trapped; aged >1 day	15	15	--	--

[1]/ Five of the 8 distended with fluid and food--no gas.

Unfortunately the measure of proventriculus distention used is not very accurate. The inherent variability in proventriculus morphology allows some proventriculi to be classed as distended even when they appear to lack internal pressure. Another flaw in this measurement is the possibility of change in distention during embedding and/or dissection. Still another error is the possibility that distention to the beetle's response systems could be any increase in pressure following the exit of food from the lumen. In this case our system of classifying degrees of distention is inadequate.

An experiment was designed to circumvent these weaknesses. The proventriculi of 10 beetles were distended artifically to see if this would change the chemotaxic response of the beetles in the laboratory olfactometer. Proventriculi were distended with water forced into the bucal cavity through a fine pipet. The pressure was supplied by a $\frac{1}{4}$ cc. tuberculin syringe attached to the micropipet.

Results of this experiment were inconclusive because the treatment was too harsh. Change in response of test beetles could be attributed to injury or to the effect of distention.

ROLE OF FLIGHT EXERCISE

The search for indicators of host-finding predisposition failed. No reliable indicators were found. None of the findings of Graham with Trypodendron seem applicable to the western pine beetle on the basis of the experiments described above. The question arises, is there a period in the ontogeny of an emerged beetle when it is maximally predisposed to respond to its prospective host? This question is difficult, perhaps impossible to answer. One part of it, the role of flight exercise on selection predisposition, is more amenable to research. Also the role of flight exercise could be the most important part of the question. It could explain the difference in response to attractive traps between trapped beetles (with flight exercise) and cage-emerged beetles (without flight exercise).

The following experiment was repeated seven times to study the effect of flight exercise on selection predisposition. Forty to sixty beetles emerged the previous day from the same brood and were divided into two samples of equal numbers. One sample was given flight exercise, the other was not. Then the response of both samples were tested by releasing the beetles out of doors near the attractive traps. The number of beetles recovered in the traps was taken as a measure of response difference.

Beetles were given flight exercise by suspending them individually on an 8-inch thread. The thread was glued to the dorsal surface of the pronotum with colorless fingernail polish. Special care was taken to make sure the only suspensory filament was a fine strand of nailpolish running antrad and dorsally from the anterior margin of the pronotum. The flight response of beetles tethered in this way varied. Some flew virtually continuously while some did not fly. Some flew intermittedly for extended periods while others started and stopped. The flight of each beetle was recorded every 20 minutes to keep track of this variability in "flight exercised" beetles.

In addition to these field flight tests, beetles with and without flight exercise were compared on the basis of response to the attractant in the laboratory olfactometer and on the basis of proventriculus distention. In both these tests 40 beetles were used; 20 were allowed flight exercise and 20 were held in capsules as controls. Beetles were tethered for $1\frac{1}{2}$ days with 12 hours of favorable flying conditions in the chemotaxis test and $\frac{1}{2}$-day with 4 hours of favorable flying conditions for the morphology test. Other procedures were the same as described above.

Only one of the 396 beetles released was recovered in the field flight tests. One hundred and ninety five of the released beetles were "flight-exercised" for periods ranging from 0 to 7 hours. Two hundred and one were controls. Percent positive in the walking chemotaxis was 79 for the flight-exercised beetles and 55 for control beetles. This difference is probably not meaningful because tethered beetles age faster than controls. The change in response associated with partial aging (days 0 to 3 or 4 of table 1) probably accounts for the measured difference. The degree of proventriculus distention was 8 positive, 2 intermediate and 9 negative for flown beetles, and 11 positive, 2 intermediate and 6 negative for unflown beetles. Flying time was short enough that differential aging rate did not greatly influence the results.

These tests failed to demonstrate an effect of flight exercise on flight predisposition.

One criticism that can be made of these tests is that beetles were not flown long enough to reach the point of response change. It comes from the idea that host selection is made only when the beetles near exhaustion. Two types of data help to refute this criticism. One, 3 of 12 trapped beetles flew for more than 3 hours when tethered. Two, trapped beetles successfully make a second flight (see above). Still these experiments may fail in other areas. For example, the type of flight exercise is different from normal flight. Tethered beetles respond predominently to escape from the thread. Change in environment immediately surrounding the beetle such as light patterns, air currents, temperature, etc. differ in tethered and normally flying beetles.

The results of the experiment to show the effect of flight exercise are in agreement with those designed to find indications of host selection predisposition in that no evidence was found to support similarity in selection predisposition between the western pine beetle and Trypodendron. This does not mean that there is no similarity, but it does suggest checking alternative explanations for poor returns of cage-emerged beetles.

ATTRACTIVE TRAP CATCHES OF INSECTS OTHER THAN RELEASED BEETLES

The attractive traps were run daily during the hours above 60° F. to supply test beetles. A daily record of the catch was kept to learn something of the possible causes of day to day variations and consequently more about flight biology. A Forest Service weather station approximately 70 yards from the traps supplied some atmospheric measurements which could have been associated with day to day fluctuations in beetle catches. Only three measurements were examined closely: barometric pressure at 8:00 a.m.;

maximum daily temperature; and miles of wind per day at 8:00 a.m. to 8:00 a.m. of the following day. The anemometer used did not respond to winds below about 5 m.p.h. as it had long arms tipped with large, heavy cups. It was 6 feet above the ground. Under the summer wind conditions at the Stanislaus Branch this anemometer might be considered more a gust counter than a true anemometer. Comparison of wind speed measurements at the location of the anemometer and the traps showed the anemometer to be in the windier location.

When the day to day change in these measurements of atmospheric conditions are compared with the day to day change in beetle catch some apparent associations are found (table 3).

Table 3.--Association of day to day change in catch with day to day change in temperature, wind, barometric pressure, and emergence of caged beetles

	Direction of change equal	Direction of change unequal
Temperature	13	12
Barometric pressure	11	9
Wind	9	1/ 19
Emergence of caged beetles	20	2/ 6

1/ $X^2 P = <.1, >.05$

2/ $X^2 P = <.01$

In the case of wind, the direction of change possibly disagrees on more days than it agrees (X^2 $P = <.10$ & $>.05$). That is, as the wind increases, catches may tend to decrease. The most obvious interpretation is that high wind velocities directly inhibit the flight or flight success of the western pine beetle. But even on the windier days the wind speed in many places 5 feet above the ground (exclusive of large openings) was < 2 m.p.h., hardly enough to inhibit a moderately strong flyer like the western pine beetle. If "miles per day" is taken as a measure of gustiness another interpretation emerges. Previous work (Vité and Gara 1962; McMullen and

Atkins 1962[4]) indicates that Dendroctonus bark beetles fly upward toward an attractive source. Regardless of the primary guidance stimulus, wind direction or attractant gradient, more complex wind movement would complicate guidance. In a multistoried stand with openings, such as the study area, gusts would obviously increase the complexity of the wind movements and attractant gradients. The author believes the latter interpretation to be more realistic than the former.

Temperature and barometric pressure like wind are represented by incomplete abstractions, daily maximum, and one daily reading in the morning respectively. Therefore, it is not surprising that incidence of equal direction of change do not differ from incidence of unequal change (table 3).

Emergence of beetles from caged material appears to be associated with catches (table 3). On days when catches increased emergence increased, and on days when catches decreased so did emergence. Three interpretations can be made: (a) beetles were escaping from cages and flying to traps; (b) the emergence of wild beetles was mirrored by emergence of caged beetles, and catch of wild beetles was an index of prevelence; or (c) both of these conditions prevailed. Some beetles did escape from the cages which were approximately 400 yards from the traps. Beyond this little can be said regarding which interpretation is most realistic.

This association suggests an interesting possibility concerning the flight biology of the western pine beetle; namely, that the beetle makes its host-finding flight the day it emerges. This would be true if any of the three possibilities above were true, but there is a fourth case in which it would not be true. Cage emergence could mirror host-finding activity of previously emerged beetles in nature.

In addition to the western pine beetle, other insects were caught in the flight traps. Some of these catches were purely adventitious while others represent attraction. No effort was made to separate these two classes other than to arbitrarily keep insects which are known to be found on trees recently killed by the western pine beetle or similar substrates. Such organisms depend on these substrates for their survival or for the survival of their progeny. Therefore, the capture of these species in the attractive traps might mean they exercised chemotaxis in response to the female western pine beetle attacks plus the logs.

All three common insect predators of the western pine beetle, Temnochila virescens var. chlorida (Mann.), Enoclerus lecontei (Wolc.), and Enoclerus sphegeus (Fabr.) were caught, as was Roptrocerus sp., a parasite of the western pine beetle. This apparent attraction has many inplications. For example, infested logs sprayed with insecticides could attract and kill many of the beetle's natural enemies. Or, a surplus of natural enemies in one area could be attracted and trapped and moved to an area where they might be more beneficial to man's interest.

4/ McMullen, L. H. and Atkins, M. D. On the flight and host selection of the Douglas-fir beetles Dendroctonus pseudotsugae Hopk. (Coleoptera: Scolytidae) Canad. Ent. 94: #1309-1325, illus. 1962.

Many insects which attack recently killed trees were caught. The survival advantage of the capacity to respond to fresh western pine beetle-killed trees is high. If this apparent attraction could be interfered with problems resulting from the attacks of these secondary invaders (round and flatheaded borers) could be minimized.

A few primary insects other than the western pine beetle were caught. Their apparent response may indicate a mechanism of survival at very low population levels. When there are too few of their own species to prepare a suitable substrate for reproduction they can be attracted to and breed in trees made suitable by another species.

MODIFICATION OF THE TECHNIQUE TO MEASURE HOST-FINDING SUCCESS

The original technique to measure differences in capacity of beetles to reach their hosts was changed in hopes that more released, caged-emerged beetles would be recovered. The catches of wild beetles seemed low in comparison to the prevalence of recent and current western pine beetle damage in the area of the traps. Unless catches of cage-emerged beetles could be increased the technique would have to be abandoned as a possible technique for comparative host-finding flight capacity studies. Two possibilities could contribute to this apparent low attraction: (a) the bait was not attractive enough or (b) the movement of attractant in the local winds was so complex few beetles could follow the attractant to its source. The technique was altered to correct these possible weaknesses by: (a) increasing the attractive charge and the volume of air exposed to the attractive charge, and (b) moving the attractive traps to a locality where local wind movement was observed to be simpler. A third modification in the original technique involved the handling of test beetles. Beetles were aged overnight or for $1\frac{1}{2}$ days in the refrigerator at 40° F. instead of aging overnight or longer under laboratory conditions (50° to 70° F.).

Once the modifications had been made both the catches of wild beetles and of cage-emerged beetles increased. Average daily catch of wild beetles was 10 for the 5 days in the new site and only 1 for the previous 5 days in the old site. The average return of cage-emerged beetles was 3.4 percent in the new site and less than 1 percent for all previous tests in the old site.

The design of this experiment precludes any indication of how much each modification contributed to the increased catches. But some relevant comments can be made from the results of other tests and measurements.

Effect of increased charge.--Data on walking chemotaxes in the laboratory olfactometer show the effect of increased attractant concentration. More beetles respond positively in increased concentrations while no repellent quality in the attractant was observed. This would suggest that increased concentration in the field traps could increase their catch.

Effect of new locality.--As discussed above, the day to day change in catch may be associated with day to day wind gustiness. The complexity of local air movements theoretically could be the mechanism of this association. If this is true, higher yield would be expected in the new locality due to its observed, simpler wind movement.

Effect of refrigeration.--If refrigeration slows the aging process then the refrigerated beetles were the physiologically youngest beetles tested.

A test designed to show the effect of aging on recovery of released beetles in the field was designed and executed. Beetles which had emerged from the same population on different days were aged under laboratory conditions and released simultaneously near the attractive traps. None were recovered at the traps but some were recovered at the release point (table 4). Many of the beetles recovered at the release point attempted to fly but could not. The debilitating effect of age is readily apparent from the results of this test.

Table 4.--Effect of aging on beetle flight capacity

Days after emergence	Number released	Number recovered at release point	Percent recovered at release point
2	48	9	19
6	50	24	48
10	38	24	63

The question arises, does aging have a similar debilitation effect on the beetle's capacity to respond or navigate to the attractive source? Under such an effect a beetle released the day after emergence might tend to be less successful in host-finding than a beetle released immediately after emergence.

An apparent realization of this possibility is reflected by the data in table 5. Proportionately, more wild, trapped beetles were recovered when they were released within an hour of their trapping than were recovered if released 1 or 2 days after trapping. The data in table 5 are not comparable in the strict sense because they were collected at different times under different conditions. The data for beetles aged 1 or 2 days are from two tests on different days in late June. The data for beetles aged 1 hour or less were taken over a 7 day period in late July. Changes in local atmospheric conditions or in the attractiveness of the traps could account for the differences indicated.

Table 5.--Recapture of trapped wild beetles

	Number released	Number recovered at trap	Number recovered at release point
Held 1 or 2 days	43	2	4
Released within 1 hour of trapping	19	11	0

From the fragmentary evidence above it appears that all three modifications could have helped increase catches.

AN ALTERNATIVE HYPOTHESIS

When the failures to find any change in host-finding predilection are considered with the possible debilitating effect of age, a new image of the host-finding flight emerges. Perhaps beetles are ready to respond to attractance and make their host-finding flight immediately upon emergence instead of requiring some preconditioning period after emergence. Aging, predators, and the random mishaps of the environment can make such a period a dangerous luxury. This new image is consistent with all the observations and test results mentioned above with the possible exception of the change in response to attractants through time in the laboratory olfactometer. More beetles were positive 1 week after emergence than the day they emerged. This apparent change in response could be an artifact of the way in which the response was measured. A walking measurement of a normally flying response could be erroneous because response to take flight can compete with the walking response. This appeared to be the case in the laboratory olfactometer. The recently emerged beetles classed as "indifferent" generally attempted flight and were strongly attracted to light. According to this new hypothesis the proportion of positive responses of flying beetles would decrease with time deleterious effects of aging. Therefore, the change in response with time does not have to be inconsistent with the new hypothesis.

ALTERNATIVE METHODS OF COMPARING THE RELATIVE CAPACITY OF POPULATIONS TO REACH THEIR PROSPECTIVE HOSTS

The field flight technique is still not perfected. At present, it is time consuming and subject to whimsey of the weather. Perhaps some simple laboratory test of flight could be used to substitute for field tests. Such tests would not attempt to separate beetles which would make successful host-finding flights from those that would not. Instead, they might measure some differences in beetles which could point the way for research on the causes of differences in vigor.

Two such tests the "tether test" and "toss test" were initially investigated. In the former, beetles were tethered as described above in the methods section for the flight exercise test. Tethered beetles were numbered and flown until they would not fly anymore. Observations were made every 20 minutes during the hours of flight, and the number of each individual beetle flying was recorded. At the end of the test the number of times observed flying was totaled for each beetle. This number was then divided by three to give total hours of flight.

The toss test consists of throwing individual beetles up into the air indoors to separate "flyers" from "nonflyers." Beetles were tossed three times before they were classed as nonflyers. Generally, the beetles flew toward a single light source, a window, and were recovered on white sheets spread under the window, and flown the following day.

Results of the two tests were compared in the following way. Twenty-five beetles were dissected from the bark just prior to their emergence and tethered until dead. Forty beetles were dissected from bark from the same tree 2 days later and toss-tested every day until dead. Twenty of the 25 tethered beetles (80 percent) flew and 32 of the 40 tossed beetles (80 percent) flew. These results seem comparable with regard to the number of beetles classed as flyers. This was substantiated in a second comparative test. Fifteen beetles were tossed and then tethered. The performance of each beetle was kept separately. Both tests gave the same results.

The two tests appear to be comparable in the total number classed as flyers, but the tether test gives some additional data for the added labor involved. For example, of the 25 beetles tethered above 7 did not fly or flew <1 hour, 6 flew 1 to 3 hours, 7 flew 3 to 7 hours, and 5 flew >7 hours. If these data on flight duration have any meaning in nature, they suggest that the average beetle can fly an appreciable distance and that individuals vary greatly in their flight capacity. (The average beetle flew >3 hours. If it could fly 3 hours, at about 3 m.p.h. it would cover 9 miles.).

Comparative toss tests were run on different populations. Cage-emerged beetles <1 day after emergence were tossed daily until they flew or died. Results are given in table 6. This type of test could be made more sensitive by including other criteria such as speed of takeoff, strength of flight, and accuracy of guidance to the light source.

Table 6.--Number of beetles flying in six toss tests

Population	Tested	Flew first day	Delayed flyers	Total flyers	Percent total flyers
F, early	50	49	1	50	100
F, late	37	36	0	36	97
G	50	38	2	40	80
H	50	44	4	48	96
I	65	60	0	60	92
J	50	45	0	45	90

Little can be said about the meaning of these tests in nature because they measure flight power only, not the quality of the guidance system under natural conditions. However, the 20 percent of population G which did not fly could not fly. Obviously, they would not be able to fly to new hosts in nature.

It is interesting to compare the results of these tests with the western pine beetle to those with the Douglas-fir beetle (Dendroctonus pseudotsugae Hopkins) reported by Atkins. (However, the methods and therefore the results, are not strictly comparable.) Results of tether tests with the Douglas-fir beetle (Atkins, 1961)5/ are in general agreement with those above in that: (1) there is a wide range of variation in this expression of flight duration; and (2) some beetles appear to be capable of long flights. The results of toss tests with the Douglas-fir beetle (Atkins, 1959)6/ also agree in that not all beetles are capable of flight.

5/ Atkins, M. D. A study of the flight of the Douglas-fir beetle Dendroctonus pseudotsugae Hopk. (Coleoptera: Scolytidae) III Flight Capacity. Canad. Ent. 93: 467 - 474, illus., 1961.

6/ Atkins, M. D. A study of the flight of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. (Coleoptera: Scolytidae) I. Flight preparation and response. Canad. Ent. 91: 283-291, illus., 1959.

SEXING LIVE WESTERN PINE BEETLES

To find a useful method of sexing live western pine beetles, brood adults from five different populations were sexed using five different criteria. They were configuration of frons, configuration of seventh tergite, stridulation sound, stridulation movement, and sex of gonads. The gonads were taken as the standard. The data (table 7) show that sexing by the seventh tergite is most accurate; however, it might be injurious to live beetles. Sexing by the configuration of the frons requires some training but can be quite accurate, especially if the few intermediate forms which exist are removed from the sample or sexed in another way. If only males are wanted stridulation sound can be used. Stridulation movement is too inaccurate to be of general use. The frons configuration is probably the fastest of any of these methods to use.

Table 7.--Number of errors made in sexing adult beetles with different methods. Basis: 341, 208 ♂♂ and 133 ♀♀

Method	Number of errors	Error percent of trials	Source of error: ♀♀ called ♂♂	Source of error: ♂♂ called ♀♀
Seventh tergite	2	.59	1	1
Frons	8	2.34	5	3
Stridulation sound	33	9.68	1	32
Stridulation movement	50	14.65	29	21

DISCUSSION

The results of this exploratory research demonstrate amply that our original plans to measure host-finding success were inadequate largely because the attractive traps did not trap enough test beetles. They emphasize the importance of planning further research to correct the difficulties encountered this season. And they provide tentatively, at least, the following working assumptions:

1. Improved caging is needed to achieve no escape, ease of collection immediately after emergence, uniform rearing conditions.

2. Paint probably not too great an interference.

3. "Saturation" of chemoreceptors probably no problem.

4. Effect of release point or recovery, especially on cage-emerged, needs investigation.

5. The field performance test works well with wild, trapped beetles but not with cage-emerged beetles.

6. Phototaxis, chemotaxis, and degree of proventriculus distention are probably not useful indicators of host-finding flight predisposition.

7. Flight exercise in the sense of prolonged flights does not appear to be the key to understanding the difference between wild, trapped beetles and cage-emerged beetles.

8. Trap location, amount of attractive charge, and age of beetles probably all affect trapping efficiency. This area needs more work.

9. Beetles need no laboratory aging, preconditioning, etc. to predispose them for host-finding flights; instead, best flight results will be attained with freshly emerged beetles.

10. Difference in flight capacity can easily be demonstrated with laboratory flight measurements. Realistic laboratory measurements of guidance capacity are more difficult to obtain.

There are some other interesting areas for research in addition to the above recommendations to improve the field, host-finding performance test. Primary among these is the development of a standard beetle. If the majority of caged-emerged adults are biologically ineffective, then the mean beetles of our test populations are also ineffective. Also the wide range of variability encountered in natural test populations may hide some intrinsic differences. Both of these complications might be overcome by producing a standard beetle free from the variability introduced by internal parasitism and nutritional deficiencies. Beetles reared in an artificial medium from

surface sterilized eggs would have these characteristics. A standard beetle would then be used as a reference point to calibrate performance tests and define biological inefficiency. The medium developed to rear these standard beetles could be used as a performance test to measure the quality of progeny.

Another possible area for research lies in the question, are good performances in one natural test good in another natural test? If simple performance tests of capacities could establish that a good performer in one test is good in another test it would help in two ways: (1) it would add confidence to the interpretation of a given performance test, and (2) it would help to concentrate work on one test to measure all capacities. This would greatly speed the "exploration for differences" part of the problem.

Should a performance test to measure the capacity of beetles to reach their host trees be sought in the laboratory or in the field? This summer's results do not seem to contradict the decision in the problem analysis to concentrate on field measurements, nor do they preclude further laboratory measurements. At this time it seems advisable to direct more effort on the field approach but to continue simple laboratory tests of different populations.

Effort to improve the field performance test should be first spent on the above suggestions to optimize return of released beetles, and then, on exploring differences within a population. Then difference of performance attributable to sex, origin on tree, parent adult or brood adult, and time of emergence in relation to other beetles of the same brood should be established. Then comparative performance tests can be made among different populations.